

The Display of the Blue-backed Manakin, *Chiroxiphia pareola*, in Tobago, W.I.^{1, 2}

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(Plates I-III, Text-figures 1-3)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest preserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe, *Zoologica*, 1952, 37 (13): 157-184.]

There have recently been several contributions to our knowledge of the extraordinary joint displays of manakins of the genus *Chiroxiphia*. Something is now known of all four species. Wagner (1945) and Slud (1959) have reported on *C. linearis*; Lamm (1948), Snow (1956), Junge & Mees (1958), Gilliard (1959) and Sick (1959) on *C. pareola*; Friedmann & Smith (1955) briefly on *C. lanceolata*; and Sick (1942 and 1959) on *C. caudata*. *C. linearis*, *C. lanceolata* and *C. pareola* are closely related, allopatric forms, together comprising a super-species, while *C. caudata* is more distinct and its range overlaps that of *C. pareola*. Correspondingly, the first three have rather similar displays, while that of *C. caudata* is more distinct. In the first three species,

pairs of males perform a synchronized dance, alternately jumping up and uttering while in the air a vibrant, growling note; whereas in *C. caudata* several males engage in a joint dance, the details of which, though the published accounts are discrepant, appear to differ considerably from anything found in the other three species.

For the Blue-backed Manakin of Tobago, *C. pareola atlantica*, which forms the subject of the present paper, Gilliard's observations have added significantly to my earlier account, and I myself have returned three times to Tobago to watch and film their displays and record their calls. The accounts by Lamm and Sick of the display of the northeast Brazilian population (subspecies *pareola*), brief though they are, indicate that their display does not differ in important respects from that of the Tobago population. Nothing is known of the displays of the populations of the interior of South America (subspecies *napensis*, *regina* and *boliviana*).

Chiroxiphia pareola is one of the largest of the manakins, and *atlantica* is the largest of its subspecies; adult males weigh from 20 to 25 gm. The adult male is black, with a flat red "skull-cap" somewhat triangular in shape with two backwardly projecting lateral horns, and a sky-blue patch on the upper back (Text-fig. 1). The legs are pale orange. The female is olive-green. Young males are green, but by the age when they begin to visit the display perches they show a certain amount of red on the crown and sometimes some blue on the back. The genus *Chiroxiphia* is characterized by the specialized outermost primaries. In the male only, the three outer primaries are pointed, the shafts being thickened and the barbs reduced. It is, however, not clear

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TEXT-FIG. 1. Adult male Blue-backed Manakin, uttering the invitation call. (Drawn from movie film.)

in what way, if any, these specialized feathers are used in the displays. The only undoubted mechanical noise, a soft click made on taking off, could hardly be made by them. It may be that the slotted wing-tip is aerodynamically important in the fluttering jumps that are the most important element in the display.

Slud's admirably clear account of the song and dance of the Central American *C. linearis* has shown how conflicting may be the different published accounts of the display of the same species of manakin. This has been partly due, no doubt, to inaccurate observation of complex and often rather quick movements, and especially in the older accounts, to reliance on memory rather than on detailed notes made at the time. Partly it results from the different observers having seen different fragments of a complex and varied pattern of display, complex in that many different display movements and postures are involved, varied in that the organization of a display sequence depends much on the circumstances and status of the individuals taking part. For *C. pareola* in Tobago there is, compared with *C. linearis*, a notable absence of conflicting observations, though much remains to be done to clarify the social relationships of the displaying birds. The display appears variable, and is so, but this variability is in the arrangement and coordination of display elements which are themselves highly stereotyped. A movie camera is extremely valuable for providing an accurate portrayal of these postures and movements, and a tape recorder for providing an objective transcription of the sounds accompanying them. These I have attempted to present in the following pages.

As usual, I am most grateful to my wife for help with the field work, especially in the tape-recording and in maintaining longer watches at the display perches than would have otherwise

been possible. I wish to thank Professor P. P. Kellogg, Dr. R. C. Stein and Mr. C. A. Sutherland, of the Laboratory of Ornithology, Cornell University, for their help and advice, and Mr. Sutherland especially for making the sonagrams. I also acknowledge with gratitude grants from the National Science Foundation.

THE DISPLAY PERCHES

Blue-backed Manakins display on bare sticks or stems in the forest undergrowth, usually two to five feet above the ground. Display perches may be sloping or horizontal, straight or curved, but most of those seen were slightly sloping and convexly bowed. Sometimes a small group or cluster of perches is used. Between bouts of displays the birds peck at the bark, which they also wear smooth with their continual perching and hopping, and they pick in flight at the leaves surrounding the perch. When they have pulled off a piece of leaf, they typically return to the display perch before dropping it.

In April, 1959, the same display perches were found to be in use as had been used in July, 1958, in forest near the top of Pigeon Peak. Also a display perch which was watched in April, 1959, in secondary forest nearer the coast was still in use in July, 1961. This was the area which Gilliard had watched, and where he was told that manakins had been dancing for decades. Thus there is little doubt that the display grounds are permanent, and that the same display perches normally remain in use as long as the surrounding vegetation is unchanged and the perches themselves remain suitable.

Gilliard suggests that the primary function of the clearing of leaves from the vicinity of the display perch may be defensive, in preventing the close approach of unobserved predators. He further suggests that it may have value in increasing the amount of sunlight penetrating to the perches and so enhancing the effect of the bright red and blue of the male's plumage. The clearing of obstructions from the area of a display perch or court is probably widespread in manakins, being known also in *Manacus* and three species of *Pipra* (Snow, 1962, a and b); in the related Cotingidae it occurs in the much larger Calfbird *Perissocephalus tricolor*, which has its display perches in the canopy of forest trees (B. K. Snow, 1961). The evidence strongly suggests that the habit of spending hours in conspicuous display does not in fact expose manakins to heavy predation; for *M. manacus*, the annual mortality of adult males was found to be only 11%, an exceptionally low figure for a small passerine bird (Snow, 1962 a), and the mortality of *Pipra erythrocephala* seemed to be

similar (Snow, 1962 b). I suggest that the primary function of leaf-clearing in all these species is to keep the display perch or court clear of the growing vegetation, so that the site remains permanently suitable for display. A further advantage is that such places will be more conspicuous than if they were screened by the surrounding vegetation. Secondarily, as Gilliard suggests, such stripping of the vegetation may, by allowing more light to penetrate, enhance the colors of the displaying bird.

CALLS AND MECHANICAL SOUNDS

Invitation Calls

Three calls may conveniently be grouped under this heading, in that they are uttered by males sitting by themselves, and appear to serve as invitations to neighboring males to join them in display, or perhaps in one case, to females to do likewise. Rigorous examination of their functions was not possible under the conditions of observation.

The chief of these calls is a rolling churr, "chrrrrr," often followed by one, two or occasionally three abrupt, rather explosive notes sounding like "chup" (Plate I, fig. 1). Typically, this call is uttered by a solitary male perched 20 or 30 feet up in the area of a display perch, and it seems very clearly to be used to attract another male to come and call with it in unison (see next section). Though they are often uttered in sequence, either the "chrrrrr" or the "chup" may be uttered by itself; in such cases single "chups" may be repeated at the rate of up to 20 per minute, and the rolling churr at rather longer intervals. (Gilliard describes this call as a "wren-like 'wwwrrrr', drawn out and ascending, and ending with an explosive 'churr' or 'chow', which was sometimes twice repeated").

The second invitation call is a single "whee" or double "whee, whew" (using Gilliard's phrasing), the first note being sharp and incisive and the second less loud and lower-pitched (Plate I, fig. 3). This call is uttered by males perched by themselves, not usually on the main calling perches, but between flights from one perch to another round the display area. Anthropomorphically, it seems to indicate restlessness and the desire to attract another bird.

A much less common call than those just described (and for this reason unfortunately not recorded on tape) was a double "coo-ee" or "joy-ee," the first note low and musical and the second sharper. (This call is described by Gilliard as "chew-wheat"). Gilliard refers to it as an invitation call, and the first call of the day. My notes suggested that it was sometimes associated with

the presence of a female, especially in one case where a male uttered it continually, and no other call, for several minutes near a display perch after a female had appeared near by. But it was heard too seldom for any safe generalization.

Synchronized Calling

When, after calling the "chrrrrr-chup," a male has been joined by another, both perch close together, sometimes side by side and nearly touching, and utter a series of perfectly synchronized ringing phrases, sometimes for minutes on end. Each phrase consists of one to five "chups" quickly repeated (Plate I, fig. 2), three being the commonest number, and the phrases themselves are repeated at the rate of 30 to 45 per minute. In the course of each bout of synchronized calling there is a tendency for the length of the phrases to increase, as shown in the following count of phrase-length in a complete bout of calling, divided into three periods:

		Number of phrases		
		1st	2nd	3rd
		period	period	period
Number of "chups" per phrase	5	—	—	1
	4	—	2	3
	3	6	11	2
	2	7	4	—
	1	1	—	—

I watched pairs of males calling thus on many occasions and was always struck by the apparently perfect synchronization of the opening and closing of their beaks, which was the more striking as the intervals between each phrase varied somewhat and each phrase, as already mentioned, might consist of one to five notes. In fact, the sonagram shows that one bird called about 0.04 or 0.05 seconds later than the other. It is especially interesting that slight individual differences in the form of the "chup" note show that the bird which called first was the one that had previously been recorded giving the invitation call (the "chrrrrr-chup") above the display perch.

On one occasion two birds came together, but began to call when they were still several yards apart and continued to do so for some time. At this unusual distance their calls were very poorly synchronized, indicating that synchronization depends on one of the birds being able to detect slight intention movements in his partner. Once only, three birds were seen calling together, when two adult males were perched close together calling synchronously and an immature male joined them, perched about two feet away,

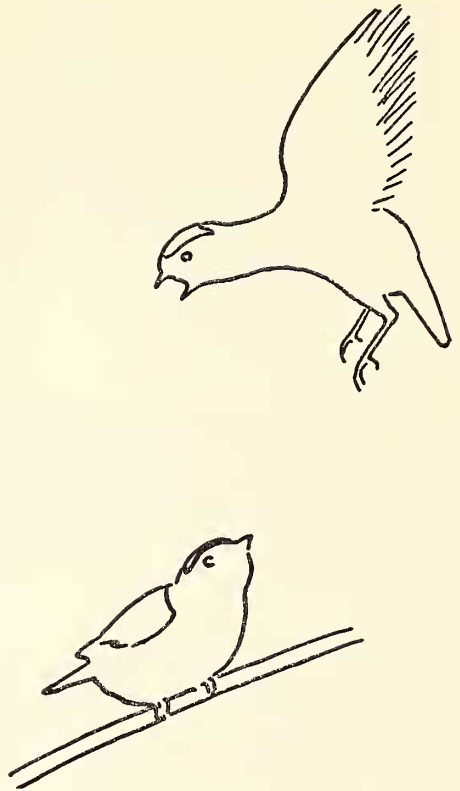
and called for some time in unison with them. (Gilliard aptly described this call as a "resounding phrase that rang through the forest like the clicking of billiard balls," but does not mention that it is the synchronized call of two birds).

When one watches a single bird uttering his invitation call over and over again, the rolling churr followed by usually a single "chup," and it is then joined by another male, whereupon both break into a resounding series of "chup-chup-chups," one receives the strong impression that the solitary male is eager to utter the longer, louder phrases, but simply cannot do it without the cooperation of another bird. Frequently, after a bout of synchronized calling, both birds fly down to the display perch and begin a bout of jumping. The synchronized calling thus probably plays some part in building up the motivation for the joint display.

Two Blue-backed Manakins sitting side by side remind one of *Pipra* and *Manacus*, in which males with neighboring display perches or courts spend long periods sitting beside each other on some perch mid-way between, but there are important differences. First, Blue-backed Manakins come together to call in unison; when the bout of calling is over they part. Males of *Pipra* and *Manacus* on the other hand perform no joint activity, but simply come together between bouts of display. Secondly, whereas in *Pipra* and *Manacus* such birds, though drawn together, are still plainly antagonistic towards each other, and in *Pipra* especially they always face away from one another, in the Blue-backed Manakin they show no mutual hostility; they face each other freely, and if one turns on the perch it may turn towards the other. There seems to be no remnant of aggressiveness in their behavior on the calling perches.

Calls and Mechanical Sounds Associated with the Display

The jumping display which will be described in detail in the next section is accompanied by a vibrant twanging or buzzing call (Plate II, fig. 4). It is uttered by the bird as it hangs in the air with beak open and head pointing downward (Text-fig. 2). When, as is usually the case, two males jump up alternately, these vibrant calls succeed one another at regular intervals, and carrying surprisingly far for their volume, they are the chief means by which the observer locates the display perches. As the display proceeds and the jumps become smaller and more rapid, the calls, which start as rather smooth, regularly alternating buzzing notes, become more irregular and take on a bleating quality (Plate II, figs. 5 & 6). As Gilliard puts it, they



TEXT-FIG. 2. A pair of male Blue-backed Manakins performing the cartwheel dance; one bird hovering and uttering the twanging call, the other shuffling up the perch in a crouched position. (Drawn from movie film.)

become "very irregular and forced, as though they were purely mechanical sounds coming from a wavering toy top." It seems as if, though vocal, they are also to some extent mechanical, in that they are gradually modified by the physical exertion of the fluttering jump, and this impression seems to be supported by the fact that the smoother buzzing note, characteristic of the early stages of the jumping display, is sometimes uttered in typical form by a perched bird.

At the end of a bout of jumping, after the twanging calls have speeded up to the rapid and confused buzzing mentioned above, the display usually ends with a sudden and rather startling vocal performance. The last bird to jump utters a louder and more distinct bleating note, with the beak wide open, and this is at once followed by a quite different, higher-pitched "zeek" or "zeek-eek," repeated up to four or five times, after which the two birds at once fly off from the display perch. I was unable to tell whether one or both of the birds uttered these sharp calls, but

a single bird jumping by itself will often end its display with exactly the same sequence of calls.

That the sharp "zeek-eek" not only brings this display sequence to an end, but actually acts as an inhibitor of display, was once very clearly seen, when an adult male performed the precopulatory display, described later, to an immature male, which some of the time behaved like a female and some of the time joined the male in joint display. Four times in the course of this joint display the immature male suddenly uttered the sharp "zeek-eek," and each time, though the activity of the birds was not the same on each occasion, it was followed by a break of several seconds before the two birds resumed their display.

During the precopulatory display described in a later section, a note was uttered that was heard at no other time. This was a low twanging note, which may be written "quaaaa", uttered by the male before flying in to his display perch from another perch a few yards away. It was a call of low volume and was not registered by the tape recorder at a distance of about 25 feet.

When flying to and from their display perch, and sometimes when flying about near it, males may sometimes make a soft mechanical click at the moment of taking off (Plate III, fig. 7). The male which continually uttered the "coo-ee" call for several minutes after a female had appeared near his display perch, also made the click every time he flew, and during the precopulatory display it was made by the male when he flew in to his display perch, after uttering the twanging "quaaaa". The click is almost certainly made by the wing-feathers, but the way in which it is produced was not discovered. The narrow and rigid outer primaries do not seem to be adapted to make such a sound; in *Manacus* the specialized secondaries are responsible for the loud snap made on taking off.

THE JUMPING DISPLAY

The fluttering jump is the basic movement of this display. Before jumping, the bird crouches a little. It then jumps up with fluttering wings, the beak pointing downwards, legs dangling, and tail pointing down (Text-fig. 2), and hangs momentarily in the air before landing back on the perch. The jump may occasionally be silent, but is normally accompanied by the twanging call, the beak being opened widely.

As already mentioned, in *C. pareola* as in its two close relatives, the jumping display is typically performed by pairs of males, which jump alternately on the same perch. When the first one jumps, the other crouches, looking upwards

at it, and then itself jumps as the first bird lands. But single males may jump, though they do not usually keep up the display for very long. When a male jumps by itself, at every jump it turns in the air so as to land facing the other way on the perch. When two males jump together their movements usually become more complex and the turn in mid-air is less obvious or is altogether suppressed by the requirements of their coordinated dance.

When two males dance together, in the simplest form of the display they jump up alternately side by side, each keeping his place on the perch unaltered. But sometimes the display is less regular, and they may jump more at random to land in another place on the same perch or on another perch a foot or two away. Sometimes one bird jumps over the other. Even when the jumping is at its least orderly, the two birds jump in strict alternation. Exceptionally, three birds may jump on the same perch, but their behavior apparently does not allow coordinated dancing by more than two birds. On the only occasion when this was seen, two of the birds jumped up alternately, while the third jumped at a little distance along the perch, out of phase with them.

The jumping of two males reaches its highest pitch of coordination when a third bird (a female, or a juvenile male who assumes the role of the female; see later) comes to the perch. The two males then turn and face the third bird, and the following sequence of display develops. The foremost of the two males jumps up, and as it hovers in mid-air the other male hops up to take its place. The first bird moves back in flight and comes down to land, and as it lands the other jumps up in the same way. Thus the two males move in the form of a Catherine wheel, or cartwheel (Gilliard), before the third bird. If, as sometimes happens, the third bird retreats, backing away up the perch, the males hop up further when on the perch and do not move back so much in flight, so that the cartwheeling pair move up the perch after the retreating bird. If, as was also seen, the third bird is aggressive and moves towards the pair, they retreat, still cartwheeling. The cartwheeling display appears to be best performed on a sloping perch, with the two males facing "uphill," but it may also be performed on nearly horizontal perches.

If the third bird flies off to another perch a few feet away, the pair of cartwheeling males may follow and continue jumping in front of it; but if it moves further off they do not follow but either stop jumping or return and continue jumping on the main perch.

Cartwheeling displays were seen many times.

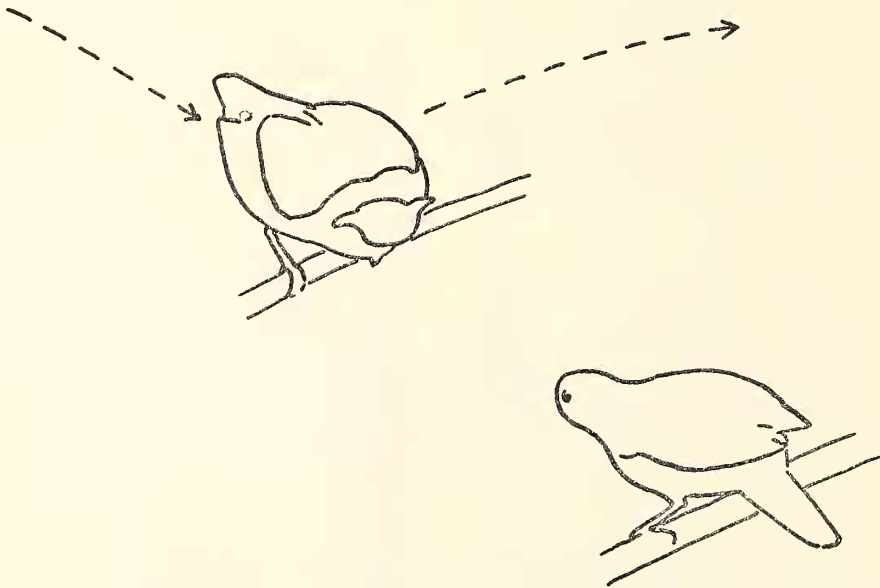
On some occasions the third bird was thought to be a female, having all-green plumage, and sometimes it was an immature male, with some red feathers in the crown. In the precopulatory display, too, as described in the following section, the female's role may be taken by an immature male. Sick (1942) found the same in *Chiroxiphia caudata*.

All bouts of jumping, whether by single males, pairs of males by themselves, or pairs of males before a third bird, usually become faster and more frenzied as they proceed. The jumps become lower and succeed one another more rapidly, until the birds are hardly leaving the perch and the alternate rhythmic twanging degenerates into "unintelligible buzzy sounds," a phrase used by Slud for *C. linearis* and equally applicable to the Tobago bird. The last jump of all is often especially frenzied; the bird turns its body rapidly from side to side as it flutters, and as already mentioned, utters a rather loud bleating call with beak wide open. Then the sudden sharp notes are uttered, and at the same instant the jumping stops and the birds usually fly off.

THE PRECOPULATORY DISPLAY

On March 30 and 31, 1959, a long sequence of display was seen between an adult male and a female, which on March 31 culminated in copulation six times. This display was stereotyped and extremely different from the jumping display described above.

It began when the female suddenly appeared on the display perch. The male then proceeded to flutter round her with a butterfly-like floating flight, crossing and re-crossing the display perch, every second or so alighting momentarily on a perch and flying on again with a buoyant, bouncing motion. In flight his wings were kept well extended and appeared to move with rapid, shallow beats, and his beak was open, though no sound was uttered. If he alighted on the display perch or some other perch near the female, he would face her, crouch for a moment with head lowered, so that the blue patch on the back was exhibited, and vibrate his wings. As his head came down, the red cap was presented squarely to the female, appearing shield-like as the two horns were extended laterally, apparently by muscular action (Text-fig. 3). The female was thus presented with a red shield surrounded by black and surmounted by a vibrating patch of sky-blue. Sometimes when the male stopped in the course of his bouncing flights and faced the female, he did not adopt this posture but merely crouched, with wings flicking. Several times in the course of this display, and on both days, the male flew out to a special perch some 20 feet from the display perch, in a direction in which he did not otherwise go, uttered a low twanging note on the perch (the "quaaaa" described above), then with a click of the wings flew back to the display perch and resumed his bouncing flight.



TEXT-FIG. 3. The precopulatory display. The male crouched, between two fluttering jumps, and exhibiting his red crown shield to the female; the female, on the main display perch, intently watching the male's performance. (Drawn from movie film.)

The female, for her part, crouched with her plumage sleeked and continually turned to face the male. Sometimes she sidled quickly along the perch, sometimes she seemed to retreat a little, but for almost the whole time she remained on the main display perch, intently watching the displaying male.

Copulation followed a set pattern. The male flew in from one side and landed for a moment on a perch near the female, who was facing him on the main display perch. He then jumped onto the display perch, landing beside the female after turning in the air so that he faced the same way as she, and mounted.

Apart from the differences in movements and postures, there were two important general differences between this display and the jumping display. First, only one male took part and no others were seen or even heard near by, though at least one other adult male and two immature males had been displaying on this perch a few minutes before and displayed at it shortly afterwards. Secondly, it was silent, except for the occasional low "quaaaa" and the soft click made when the male flew in from the special perch 20 feet from the main perch.

A few days later, an adult male, probably the same one, performed substantially the same display to an immature male (recognizable by his red cap), but the display was more confused, as the immature male behaved like a female for some of the time, crouching on the display perch and continually turning and watching the male, and sometimes itself performed the bouncing flight to and fro across the display perch at the same time as the adult male. Both birds also occasionally made quick side-to-side slides on the display perch. In July, 1961, similar display was again seen between an adult male and an immature male, whose red head-feathers were hardly showing through the green.

On several other occasions pairs of males were seen, at this and other display perches, both performing the floating flight and criss-crossing the display perch with buoyant leaps. On these occasions no females or immature males were seen near by. Thus the strong tendency of the males to display jointly extends even to the precopulatory display.

The side-to-side "slides" on the display perch, mentioned above, were seen on a few other occasions. If they were associated with any other display it was with the floating flight rather than the jumping display. The slide is actually a rapid side-stepping with very short steps; it resembles the side-to-side sliding of *Pipra* species (Skutch, 1949; Snow, 1962 b) and may be a homologous

display, but in *Chiroxiphia* it is comparatively infrequent and little ritualized.

SOCIAL ORGANIZATION

In my earlier account, I reported that the males were found to be in pairs in the forest, and that these pairs called synchronously from perches 30 or 40 feet up in the trees and came down to perform synchronized dances on the display perches. My limited observations suggested that the members of the pairs kept together for much of the time and that each pair had its own display perch, or perhaps more than one perch. Display perches of the presumed "pairs" were scattered through the forest at intervals of about 100 yards. These observations were made in undisturbed rain forest near the top of Pigeon Peak, the highest point of Tobago. Gilliard's observations, made in much drier secondary forest nearer the coast, showed a rather different picture. He found four display perches in use about 15-20 yards apart, and his observations suggested that the pairs of males that performed at them were drawn from a group of several males which jointly owned the four display perches, though there was some evidence of a social hierarchy within the group. Gilliard's group consisted of both adult males and immatures with varying amounts of red on the crown.

In July, 1958, I returned to Tobago and watched display again on Pigeon Peak. Conditions for observation were very poor, as the wet season was in full swing, and in addition display was slack, since the season of moult was approaching. The males I watched were mostly sitting calling solitarily; one was occasionally joined by another for a spell of synchronized calling and then jumping. Later a bird in immature male plumage came to the same perch but only did a few jumps and was not joined by the "owning" male, who was near by. I gained the impression that some birds had already started to moult, the "pairs" had broken up, and the few remaining adult males were giving invitation calls near their display perches but were not highly motivated to display.

In March, 1959, I returned and spent eight days in the area earlier studied by Gilliard, with a few shorter visits to the hill forest. In the former area I found three display perches in use, probably the same ones as Gilliard had found (he had taken one of the four for a museum exhibit), at which at one time or another at least eight males (four adults and four recognizably different immatures) were present. The organization appeared to be as Gilliard had described it. However, after watching carefully and trying as far as possible to keep track of individual

birds, I very strongly had the impression that the main display perch that I watched was in fact "owned" by a single adult male. This bird, if indeed it was always the same bird, spent much time calling from a certain perch about 20 feet up and several yards away from the display perch. Here other adult males would join it, and together they would utter the synchronized calls. The presumed owner would at times fly down to the display perch by himself and call there, as if trying to attract a partner. As usual, the normal jumping display developed when he was joined by another male, and more confused displays when more than one other male was present. It was at this perch that the precopulatory display described in the previous section was seen. Shortly afterwards an adult male, thought to be the one that had copulated, chased an immature male from the display perch, and the same was seen a day later. During this visit, I also saw four males (two adults and two immatures) together at a display perch on Pigeon Peak, which indicated that the situation I had found there in 1956 was not so invariable as I had thought.

Watching only unringed birds, I was unable to be certain of the identity of the birds coming to the display perches, except for some of the immature males which had different amounts of red on the cap and blue on the back. These immature birds were generally subordinate to the adults, and when they joined in jumping displays with an adult male they were occasionally supplanted by another adult. They were never seen performing the floating flight.

On my last visit, in July, 1961, I attempted to settle the question of the ownership of display perches by trapping and color-ringing some of the males in a display area. Again I chose the display area studied previously by Gilliard and myself. Three adult males and two immatures were present, but unfortunately display was slack. (There is no information on the breeding season of the Blue-backed Manakin in Tobago, but the observations made in July, in 1958 and 1961, suggest that it ends earlier than that of *Manacus manacus* and *Pipra erythrocephala* in Trinidad, in both of which breeding is in full swing in July). One of the adult males spent much time calling from the same tree as was used by the presumed "owner" in 1959, but it was only occasionally joined by another bird. There were a few bouts of jumping on the display perch (the same as was used in 1959), probably by these two birds.

After two days' watching I trapped and color-ringed two males near the display perch. One was an adult male in good plumage, which from

later observations was almost certainly the bird that had called regularly in the tree near by and the presumed "owner" of the display perch. The other was a bird moulting from juvenile to adult male plumage. The operation failed in its main purpose, as neither of the two ringed birds was seen again in the further week at my disposal, but it yielded a little information. No male was subsequently seen calling in the tree that had been occupied by the adult male, but two adults called near by on other perches, and after four days two birds, an adult and an immature male, were seen displaying at the display perch. But display was very sporadic, and it seemed that the frightening off of the "owning" male had practically put an end to display at this perch for the season.

If, as my observations suggest, there is a dominant male at each display perch, and he is joined by his neighbors for bouts of synchronized calling and dancing, further questions are raised regarding the visiting adult males: does each of them also own a display perch, to which it attracts its neighbors, or do they have a subordinate position at the display perch of the dominant male and no perch of their own? Of these I believe that the first is the more likely. It would be paralleled by the situation found in *Pipra aureola* (Snow, 1963), in which each male has a display perch but also visits his neighbor's display perches for joint display.

If one male is dominant at each display perch, some of the puzzling features of the Blue-backed Manakin's display can at least be partially explained. In the synchronized cartwheel dance by two males in front of a female, the parts played by each male are exactly equal, a situation that does not seem conducive to successful copulation by one bird. But the display that immediately precedes copulation is in fact quite different; it is nearly silent, and only one male is present. One may conclude that the noisy cartwheel dance is a more preliminary stage of courtship, whose function is to attract females and condition them to the display perch, and that when a female comes to the perch ready for copulation the visiting males are no longer tolerated, and the dominant male alone courts her and copulates with her.

But if this is so, there still remains the problem of the evolution of this kind of behavior. Males must be sexual rivals, and it is difficult to see what advantage a male can gain by helping to enhance his neighbor's display while neglecting his own display perch. His neighbors may on other occasions come to his display perch, but in either case behavior is involved which seems dis-

advantageous to the individual practicing it. A fuller understanding must come from the color-ringing and intensive observation of birds at several neighboring display perches. All the species of *Chiroxiphia* seem to be rather common in suitable habitats, and the task should not be unduly difficult for an observer resident in an area where they occur.

SUMMARY

The display of the Blue-backed Manakin, *Chiroxiphia pareola*, was watched and filmed in Tobago in the course of four visits in 1956, 1958, 1959 and 1961, and its calls were tape-recorded.

Males display on perches a few feet above the ground in forest. The birds keep the perches clear by plucking off the surrounding leaves, and the same perches are used year after year.

Three invitation calls are described, which are uttered by single males and serve to attract other males. When a calling male has attracted another, they perch close together and utter a series of perfectly synchronized, far-carrying calls. Pairs of males also perform a synchronized dance on the display perches, accompanied by a vibrant twanging note.

When a female comes to a display perch, the pair of males may dance in front of her in the same way. But copulation is preceded by a quite different display involving only one male, who crosses and re-crosses the display perch with buoyant leaps, while the female remains on the display perch continually turning and watching him. Immature males may take the role of the female in both these displays.

The social organization is not properly understood, but it is suggested that there is a dominant male which "owns" each display perch, and that the males which join him for the synchronized calling and dancing probably have their own display perches in the vicinity. The problem of the evolution of this kind of joint display is briefly discussed.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Part of the invitation call. The last five notes of the rolling churr, followed by a "chup."
- FIG. 2. A synchronized "chup-chup-chup," uttered by a pair of males sitting side by side. (The drawn-out note at approximately 6 kc. is extraneous).
- FIG. 3. The double "whee, whew."

PLATE II

- FIG. 4. The vibrant buzzing call; a short, smooth buzz uttered near the beginning of a bout of jumping.

- FIG. 5. Two vibrant buzzing calls, made by two males jumping alternately; more drawn-out than Fig. 4.

- FIG. 6. Irregular buzzing calls, made by two males near the end of a bout of alternate jumping.

PLATE III

- FIG. 7. The mechanical click, made by a displaying bird at the moment of taking off for a flight.

For further explanation see the text.